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DIFFUSION OF GENE PRODUCTS

By Karl Sax

Arnold Arboretum, Harvard University

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The phenotypic expression of a gene may depend upon its relation to neighboring genes in the chromosome, the transmission of gene products from the nucleus to the cytoplasm and the diffusion of gene products from cell to cell. Although examples of position effect are rather limited, it is clear that the effect of a gene may be conditioned by neighboring genes. This action might be attributed either to the effect of adjacent genes in the production of gene products, or to the early interaction of products of adjacent or neighboring genes. There is abundant evidence that gene products may pass through the nuclear membrane.[1] Even during the "resting stage" of a cell the genes are active in controlling cellular development, as shown by the variation in growth of microspores in triploid *Tradescantias*.[2] The diffusion of gene products from cell to cell or even to relatively remote tissues is shown by the transplant experiments of Beadle, Ephrussi and Caspari in *Drosophila* and *Ephestia*.[1] Larval eye discs transplanted to abdomens of other larvae may be autonomous in pigment development or may be controlled by the host, depending on the genetic constitution of the implant and of the host. A remarkable case of a similar nature has been found in *Habrobracon* by Mrs. Whiting.[3] Eye mosaics may have a sharp line of cleavage between the colored segments, or the colors may merge and interact at the boundary of the mosaic areas, depending on the genetic composition of the mosaic males. It is evident that certain gene products are diffusible while others are not.

The development of the microspores in certain plants provides further evidence on the diffusion of gene products. In nearly all basic diploid plants the microspores rarely develop into pollen grains if a chromosome or even part of a chromosome is missing. Due to "non-disjunction" of bivalent chromosomes at the first meiotic division the daughter nuclei are either deficient or carry an extra chromosome. The deficient nuclei undergo the second meiotic division, because the cells have been condi-

tioned for one more division cycle, but the resulting deficient microspores fail to develop. The rare occurrence of N-1 microspores which reach the stage of nuclear division has been attributed to non-disjunction at the second meiotic division.[4] In *Uvularia* the deficient microspores die if they become separated from their complementary hyperploid sister cells, but heat treatment during meiosis often causes the microspores from a pollen mother cell to remain attached. Barber[5] found that the deficient microspores in such attached cells undergo nuclear division and that the nuclear divisions in both the hypoploid and hyperploid microspores are synchronized. Apparently substances essential for growth and development are able to pass from hyperploid to deficient microspores only when the cells are attached. Barber has described similar cases in certain orchids.[6]

In the normal development of *Tradescantia* microspores there are conspicuous granules in the cytoplasm during early development. These granules gradually disintegrate and begin to disappear before the initiation of prophase of the nuclear division. In sterile microspores the granules persist and are present when nuclear division occurs in the neighboring normal cells. The sterile microspores fail to develop and are much smaller than normal microspores. According to Schmitt and Johnson[7] the granules in *Tradescantia* microspores are composed primarily of protein.

Occasionally *Tradescantia* microspores are found in which the chromosomes are separated by complete or partial cell wall formation. These dumb-bell shaped microspores have three chromosomes in each lobe and the lobes are separated by cell walls or by deeply constricted regions (figure 1). The aberrant microspores are about as large as normal cells, but the protein granules persist until metaphase. The granules had disintegrated more than those found in adjacent sterile microspores, but were very conspicuous when compared with the condition in normal microspores (figure 1). The origin of these aberrant microspores is obscure. They may be produced by non-disjunction at the first meiotic division, followed by incomplete separation of the two daughter cells of the deficient dyad, or they may be produced by the failure of the chromosomes to unite in a single nucleus at the telophase of a normal second meiotic division.

The development of attached half-microspores with only three chromosomes in each cell is not unexpected since deficient cells are conditioned for the following nuclear division. The persistence of the protein granules does suggest that the action of all chromosomes must occur to effect disintegration of the granules. Apparently gene products from the isolated groups of chromosomes cannot diffuse fast enough, especially when separated by a cell wall, to effect the complete disintegration of the granules. The growth of the cell is nearly or quite normal, however, as one would expect in view of Barber's results with attached microspores. Evidently the growth-promoting substances can pass through the thin walls of

attached microspores, but the products responsible for granule disintegration are inhibited by cell walls or perhaps even by cytoplasmic isolation. These results with plant microspores are in complete accord with the variation in diffusion of gene products found in *Drosophila* and *Habrobrachon*.

One of the most interesting cases of diffusion of gene products has been described in *Neurospora* by Dodge.[8] Two races when grown together produce a heterocaryotic mycelium containing nuclei from each parental

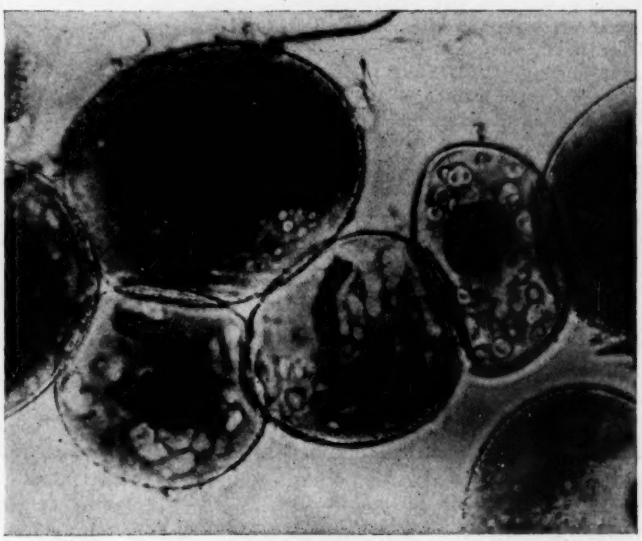

FIGURE 1

An aberrant *Tradescantia* microspore is shown with three chromosomes in each part of the dumb-bell shaped structure. Total growth is nearly normal, but the protein granules have persisted, due presumably to the isolation of gene products in the isolated chromosomes of the basic genom. A normal microspore is shown above and a sterile microspore to the right of the aberrant cell.

race. The resulting mycelium shows a great increase in growth although no nuclear fusion occurs. Dodge suggests that the growth substances produced by the nuclei of the two races supplement each other to produce the increased growth—a situation comparable to the hypothesis suggested by Robbins to account for heterosis in tomatoes. The results with *Neurospora* show that gene products necessary for growth need not be produced in the same nucleus in order to be effective, but can diffuse into the cytoplasm from different nuclei and unite in promoting increased vigor.

Summary.—Gene products essential for growth are able to diffuse between attached cells, but not between isolated microspores. The gene products necessary for disintegration of protein granules are unable to diffuse freely through a cell wall in aberrant *Tradescantia* microspores. This variation in the diffusion of gene products is in accord with the results found in insects.

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*THE EFFECT OF X-RAY STIMULATION ON THE BIOELECTRIC POTENTIALS OF THE AVIAN EGG**

BY ALEXIS L. ROMANOFF AND ARTHUR A. BLESS

AGRICULTURAL EXPERIMENT STATION, CORNELL UNIVERSITY, AND DEPARTMENT OF PHYSICS, UNIVERSITY OF FLORIDA

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Introduction.—The electrical activity of living systems has recently received a great deal of attention from a number of investigators. It is recognized that bioelectrical potentials are not merely an accidental by-product of the activity of the living organisms, but are probably conditioned by the organism and, according to some observers, profoundly influence its living processes. The electrical potentials and the electrical fields are created by ions and their spacings which are "the irreducible relatedness of the components of living things," as Northrop and Burr[1] expressed it.

The vital activity of the blastoderm of the hen's egg has been investigated recently by Romanoff and Cottrell.[2] The results have shown that the potential difference between the blastoderm and the albumen of fresh fertile eggs is much larger than the potential of infertile eggs. The electrical activity of the blastoderm is therefore an indication of the vital activity of the organism. In view of the importance of this criterion of vital activity it seemed interesting to determine the physical factors that affect the potential, and the bearing these factors have on the later life of the embryo. This paper deals in particular with the effects of x-rays on the bioelectric potential.

Experimental Methods.—About 1200 fresh White Leghorn eggs[3] were

subjected to x-ray doses ranging from 8 to 5000 r units. The radiation was supplied by a Coolidge, water-cooled, tungsten target tube with a 45° focus. The tube was operated at 55,000 volts and 10 milliamperes. The radiation was filtered with 1.2 mm. of aluminum. Under these conditions the band of radiation was fairly narrow, extending from 0.24 to 0.36 Angström units.[4] Output of the tube was approximately 600 r units per minute at a distance of 14 cm. from the target.

The apparatus used for the measurements of the bioelectric potentials has been described elsewhere.[2] The sensitivity of the system was about 20

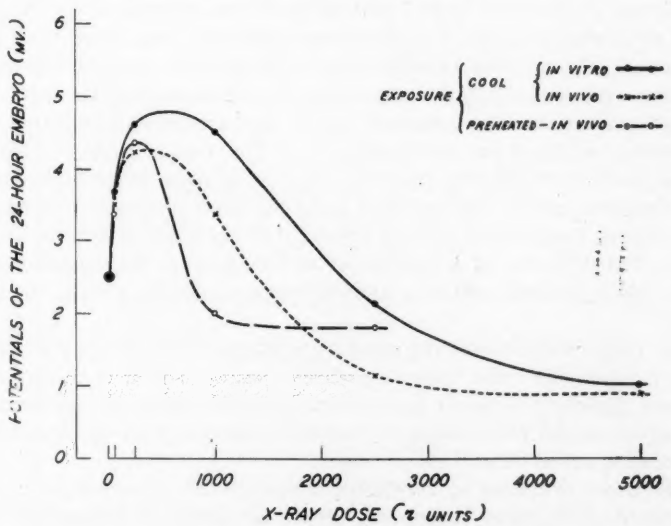

FIGURE 1

The effects of various doses of x-rays on the bioelectric potential of the 24-hour chick blastoderm.

microvolts per millimeter of scale deflection on a wall galvanometer. This sensitivity proved to be ample for the purpose.

The eggs were irradiated *in vitro*, with the yolks submerged in the albumen and held in small beakers by glass rings, and also *in vivo*. One half of the eggs irradiated *in vivo* were exposed to x-rays when cold, while the other half were preheated for three hours before exposure. The potential differences between the blastoderm and the albumen and also between the yolk and the albumen of the developing eggs were measured for 24 hours at 6-hour intervals.

Results.—Figure 1 shows the variation of the potential of the 24-hour

embryos as a function of the x-ray dosage. It is evident from this figure that x-rays influence profoundly the vital activity of the embryo. Small doses exert a stimulating effect with the maximum stimulation occurring at about 250 r units. Larger doses inhibit vital activity. This agrees with the experiments on the early growth of the blastoderm as a function of x-ray exposure.[5] At very large doses the x-ray action becomes lethal with the bioelectric potential reduced greatly, approaching the value of non-fertile eggs. The behavior of the bioelectric potential under the influence of x-rays is thus similar to the behavior of plants which are stimulated by small doses and are inhibited by large exposures to x-rays.[6, 7, 8]

It is also evident from figure 1 that the bioelectric potential of eggs irradiated to inhibitive doses of x-rays when preheated was lower than the potential of those irradiated when cold. This indicates that the biological effect of x-rays on an organism is greatest when the activity of the organism is high, which again is in agreement with similar experiments on plants.[9, 10] There is, however, an important difference. The effect of x-rays on sprouting seeds is 15–20 times the effect of x-rays on the same seeds irradiated in the dormant state.[11] On the other hand the effect of x-rays on the preheated eggs is only a few per cent greater than the effect of x-rays on cold eggs. The difference is doubtless due to the fact that the blastoderm of fresh eggs is probably not in a state of complete dormancy, as is the dry seed.

The range of doses exerting stimulating effects is greater for cold eggs, both *in vitro* and *in vivo*, than for preheated eggs. This is to be expected because the effects of x-rays on the inactive embryo are much smaller than the effect on the active embryo; naturally the range of doses exerting stimulating action on cold eggs is larger.

The effect of x-rays on bioelectric potentials of preheated fresh and incubated eggs is shown in figure 2. From this figure it is evident that the range of stimulating doses of x-rays is much wider in fresh eggs than in those incubated for 24 hours (Fig. 2 (*A*)). The relative changes in potential (Fig. 2 (*B*)) were observed to be greatest in the fresh eggs and least in those incubated six hours. A noticeable increase in potential of eggs incubated 24 hours would indicate that the general detrimental effect of x-rays becomes apparent only after a certain time[5, 12] and is followed by a period of physiological recovery. The lag of the effect may be explained in the following way.

The biological effects of x-rays are no doubt a result of the physical absorption of x-rays and the accompanying photoelectric and ionization action. The full effect of the photoelectric action with the consequent chemical changes and the biological effects become apparent only after a more or less extended period. On the other hand, while the biological effects occasioned by the x-rays are taking place, the inertial and defensive

forces of the organism combat these effects of x-rays and help the organism to recuperate from these effects. It is evident, therefore, that at a certain time after exposure the effects will be a maximum, after which the defensive and the recuperative forces will diminish the effectiveness of the x-ray doses, unless the action is lethal.

The potential of the blastoderm seems to be greatest after about 18 hours of incubation. This, however, does not mean that the activity of the

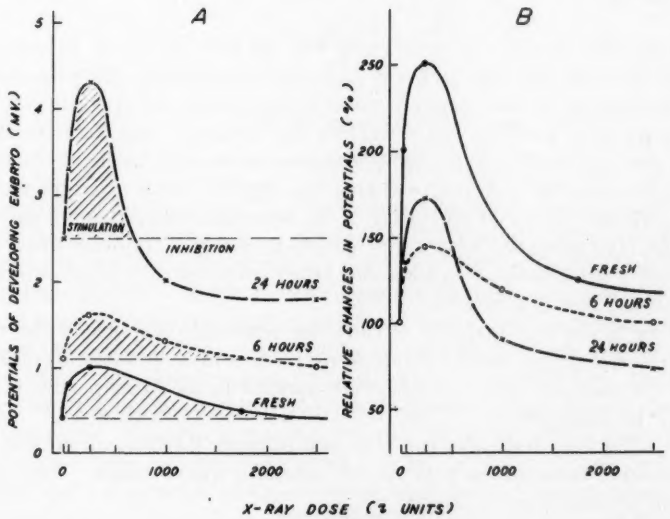

FIGURE 2

The effect of exposure of preheated eggs to various doses of x-rays on the bioelectric potential of the chick blastoderm in its early stages. *A*, potential differences in millivolts of the blastoderm of fresh eggs, and incubated six and twenty-four hours. *B*, relative changes in potential differences (control considered 100 per cent). The eggs were preheated for 3 hours at incubating temperature.

organism diminishes beyond this period. The growth of the blastoderm proceeds at a very rapid rate,[5] but because of the physiological differentiation it is not possible to speak of the potential of the blastoderm as a whole. Each part of the blastoderm definitely gives a different electrical potential. This has been well demonstrated by Burr and Hovland[13] in the study of cephalo-caudal potential of the chick embryo.

The potential difference between the yolk and the albumen is usually very small. This, however, is not always the case. A small region, about one square centimeter, was found on a number of yolks, which was charac-

terized by an extraordinarily high potential, higher than that of the early blastoderm, as is shown in the table below on a group of unexposed eggs.

	BLASTODERM	MAIN BODY OF YOLK	SMALL REGION OF YOLK
Fresh fertile eggs	0.5 mv.	0.8 mv.	2.7 mv.
Incubated 6 hours	1.3 "	0.7 "	2.9 "
Incubated 24 hours	3.0 "	0.5 "	1.3 "
Infertile	0.3 "	0.2 "	1.5 "

While the frequency of such cases was not very great, the presence of such regions in the yolk makes it undesirable to measure the potential of the blastoderm in intact eggs between two points on the opposite poles of the equatorial plane as has been done by Vorontsov and Serguijevski.[14] The potential attributed to the blastoderm may actually be due to the yolk. In most cases the high potential area was slightly darker than the rest of the yolk and the line of separation of the two regions served as a boundary of the high potential area. The potential changed abruptly when this boundary was crossed. In some cases the high potential region showed no visible differences in coloring.

Since in the vast majority of cases the potential difference of the yolk remains unchanged under various exposures to x-rays, it is safe to conclude that the electrical effects of x-rays are confined to the living portion of the egg—the blastoderm.

In some very few cases the potential between the blastoderm and the albumen or between the yolk and the albumen was reversed. The origin of this reversal is not at all clear.

Summary.—These experiments indicate that:

1. X-ray doses of about 250 r units applied to fresh eggs stimulate vital activity of the developing embryo with the increase in the potential difference between the blastoderm and the albumen.

2. The range of stimulating doses is much greater for cold eggs, than for preheated eggs.

3. Large doses of x-rays inhibit embryonic development and diminish the potential difference.

* This work was done at the Department of Physics, University of Florida.

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NUCLEIC ACID STORAGE IN THE TOAD'S EGG

BY THEOPHILUS S. PAINTER AND A. N. TAYLOR

UNIVERSITY OF TEXAS

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From chemical analyses it has been known for some time that the unsegmented eggs of a number of different animals carry a high proportion of the nucleic acid which is present at the time larvae hatch (e.g., frog 28%, sea urchin 100%).[1] Brachet[2] has shown, in the case of the sea urchin, that this nucleic acid is initially in the ribose form (ribonucleic acid) which is partially transformed into the desoxy ribose type (thymonucleic acid or chromatin) as development goes forward. The writers have been studying the cytological mechanisms by which this nucleic acid is laid down in the egg cytoplasm.[3, 4] The present report deals with the oöcytes of the toad (*Bufo valliceps*), a form of especial interest because of the enormous germinal vesicle and the presence of the so-called "lampbrush" chromosomes. In the past, both of these features have been interpretated in various ways as contributing to the nucleic acid reserve of the egg cytoplasm.

Methods.—Fresh ovaries were preserved either in Nawaschin's fluid and the sections stained by Feulgen's Nucleal method, or fixed in Helly's fluid and stained by Unna's methyl green-pyronin mixture, both before and after treatment with a ribonuclease enzyme.

Observations.—Figure 1 is a camera lucida drawing showing in the wall of the ovary an oögonial cell in prophase and two very young oöcytes in the bouquet stage (one nucleus drawn to show the chromosomes, the other the surface of the nuclear wall). In the oögonium all of the chromatin is confined to the prophase chromosomes. In the oöcytes, on the other hand, the chromatin is found in two types of structures: (*a*) the chromosomes which have the loop form characteristic of the synizesis stage, and (*b*) free chromatin granules which lie against the inside of the nuclear wall and are most numerous on the side of the nucleus opposite that towards which the ends of the chromosome loops are oriented. This distribution of the nuclear contents makes it possible to observe that there is no connection at this

time between the chromosomes and the free granules, an important point. The subsequent history of the oöcyte is best followed by considering the behavior of the chromosomes and the free chromatin granules separately.

At the bouquet stage the chromosomes appear to be made up of granules embedded in unstained material, the matrix, which imparts a rather fuzzy outline to the whole (Fig. 1). As the egg nucleus, or germinal vesicle, grows in size the chromosomes increase in length by uncoiling and reach their maximum extension when the nucleus is about 40 or 50 μ in diameter. With a further increase in nuclear size the chromosomes occupy only a limited area within the germinal vesicle. Turning to details, when the nucleus is about double its initial diameter (10 μ) at the bouquet stage, the individual chromosomes (Fig. 2 (*a*)) are still relatively thick and granular and quite jagged in outline. Part of the latter is due to the zig-zag arrangement of the chromomeres (chromioles) and part to lateral extensions of the achromatic matrix into the nuclear sap, as we interpret it forming the side branches which characterize the lampbrush chromosomes. The chromosomes are not uniform in staining reaction. There are localized areas of different chromosomes which are thicker, because the chromatic granules are larger, as indicated in figure 2 (*a*). These heterochromatic areas persist throughout the growth period. In nuclei about 30 μ in diameter (Fig. 3 (*a*)) the chromosomes are thinner and longer and the chromomeres appear to be arranged in a zig-zag manner in a mid-focal plane due to the uncoiling of the chromomeric threads of which each chromosome is composed. The side branches, which do not color with Feulgen's stain, are more pronounced. With further extension in length the Feulgen positive chromomeres assume a linear order, a condition which is retained until a contraction sets in prior to the breakdown of the germinal vesicle wall (Fig. 4). In the later stages (from 30 μ on) it is obvious that each chromosome is made up of two threads held together by chiasmata, but we have been unable to observe any split in the two threads, which the presence of chiasmata would imply.

After Feulgen's stain the chromosomes in later stages are rather difficult to observe but the chromomeres do not lose their purple color, contrary to the report of Koltzoff[8] and others. In the toad the side branches of the chromosomes are never conspicuous and are best seen with oblique illumination. When sections are heavily overstained with haematoxylin, however, we get the classic lampbrush image except for the absence of loops which we have not seen in toad eggs fixed in Nawaschin's or Helly's fluids.

So far we have been unable to distinguish oöcytes earlier than the bouquet stage and have not observed just how or when the chromatic granules are separated from the meiotic chromosomes. The former lie just within the nuclear wall, are somewhat variable in size (best shown in tangential section of the lower nucleus in figure 1) and are most numerous on the side

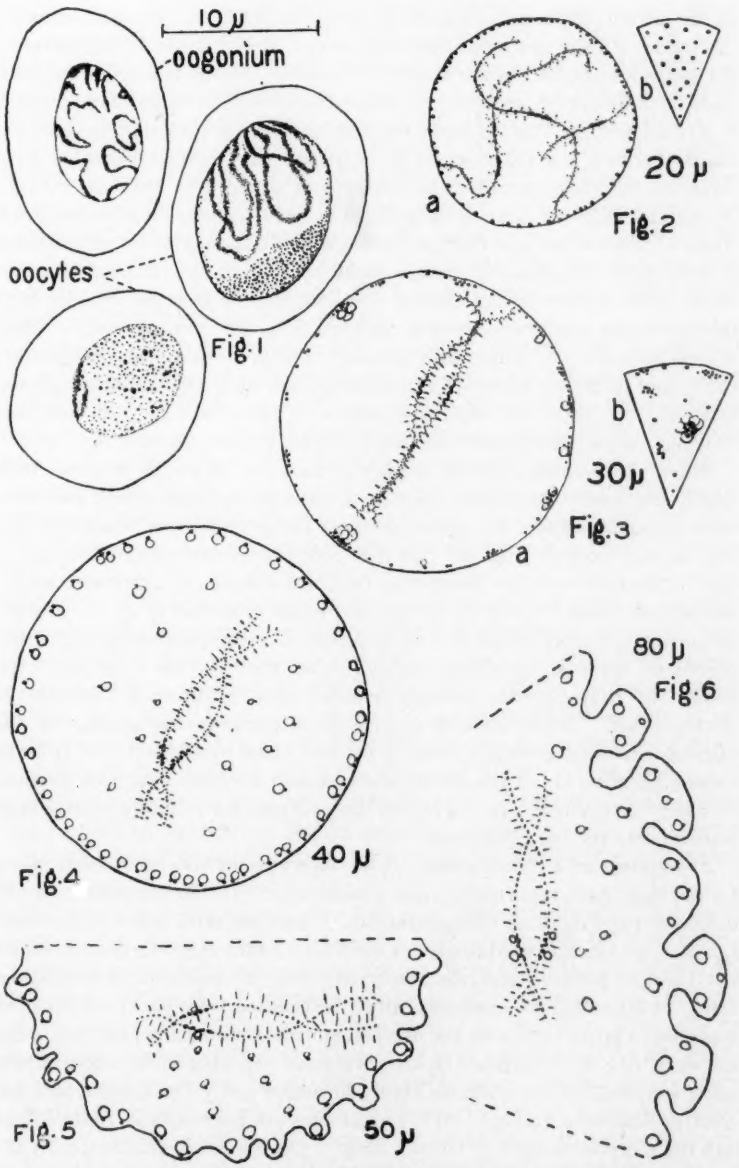

Figure 1 is a camera lucida drawing and the remaining figures are semi-diagrammatic.

of the nucleus opposite to which the free ends of the chromosome loops are oriented. As the germinal vesicle grows in size there is little change in the granules until a nuclear diameter of about 30 μ is reached when they show a pronounced tendency to associate into rather large clumps (Figs. 3 (*a*) and 3 (*b*)). This behavior suggests that the granules are heterochromatin because several workers have noted that heterochromatin from different chromosomes tends to synapse at about this point in meiosis. About this time small nucleoli begin to arise in association with the granules; clusters about the clumps, or single nucleoli against single granules. A little later the granular clumps break up and spread out and thus the whole inner surface of the nucleus becomes lined with small nucleoli with the chromatin organizers directed outward (Fig. 4). Uusually each nucleolus shows only one chromatin granule attached to it but occasionally there may be two or more. The nucleoli proper are fairly uniform in diameter at first; there are several hundreds of them and they do not take Feulgen's stain, though with haematoxylin they stain intensely.

When the germinal vesicle reaches a diameter of about 60 μ its wall, which previously has been smooth in outline becomes wavy and soon shows numerous finger-like pseudopodia or processes each of which contains one or more nucleoli (Fig. 5). We now note a good deal of variation in the size of nucleoli and the chromatin organizers begin to disappear as the nucleoli diminish in size, as if they are being absorbed (Fig. 6). In the meantime new nucleoli are seen to be arising in connection with the heterochromatic areas of the chromosomes. After they become detached, each shows the characteristic Feulgen positive granule directed towards the nuclear wall. These nucleoli appear to migrate to the surface of the nucleus. In older germinal vesicles the new crops of nucleoli tend to lie in concentric areas about the chromosomes which suggests that their production may be cyclical. We have seen no evidence for a bodily extrusion of nucleoli into the egg cytoplasm.

Experiment with Ribonuclease.—The observations recorded above were, for the most part, reported by us in December, 1940. In the same year but unknown to us (because the journal did not reach us until in 1941), Brachet[5] reported that he had used Feulgen's technique on the eggs of frogs and found the Feulgen positive granules associated with the nucleoli. In addition, using a heat stable ribonuclease, which he isolated from pancreas, Brachet was able to prove that both the nucleoli and the cytoplasm of the frog's egg are very rich in ribonucleic acid. We have repeated these experiments using a crystalline ribonuclease kindly furnished us by Dr. Kunitz, and can confirm Brachet's findings. When toad eggs are preserved in Helly's fluid and the sections stained in Unna's methyl green-pyronin mixture both the nucleoli and the cytoplasm stain a brilliant red. Some red-staining material is present in very young oöcytes and in older eggs there is a very large

amount of it with a rather sharp gradient, the color being most intense next to the nuclear membrane and shading off towards the cortex. If, now, sections are first treated with ribonuclease for a few hours, and then stained with Unna's mixture, the red color no longer shows in either the nucleoli or the cytoplasm. In control slides treated with the inactivated enzyme the staining is the same as in untreated slides. Except for a loss of staining capacity, nucleoli are not visibly affected by ribonuclease. Brachet interprets these results to mean that the red color is due to the presence of ribonucleic acid which is removed by the ribonuclease treatment. Obviously then, the heterochromatic granules and the nucleoli associated with them are part of a mechanism for the laying down of ribonucleic acid in the cytoplasm of the toad's or frog's egg.

Discussion.—Before Feulgen's technique was developed for the identification of chromatin (thymonucleic acid) it had been commonly reported that in eggs with large germinal vesicles the chromosomes, the numerous nucleoli and various unidentified nuclear inclusions, stain deeply with basic dyes. And a number of observers, noting that the amount of basophilic material which finally entered the first polar spindle (as chromosomes) was only a small fraction of the total seen earlier in meiosis, suggested that with the breakdown of the germinal vesicle wall this excess nuclear material would be available to the developing embryo (Conklin,[6] Godlewski,[7] Koltzoff[8]). The present study, however, indicates that there is a specific cytological mechanism in the toad (and frog) which begins to deposit ribonucleic acid in the cytoplasm of the oöcyte soon after it is differentiated and continues to function through the months required to build up the mature egg. While large amounts of nuclear material are set free in the cytoplasm when the germinal vesicle breaks down, this appears to contain very little nucleic acid of either the ribose or desoxy ribose type. This conclusion is supported by the observations of Caspersson and Schultz[9] that in the sea urchin the mature germinal vesicle is relatively poor in pyrimidine bases while the cytoplasm just outside the nuclear wall is very rich in them.

Within the past five years a good deal of evidence has come to light which indicates that there is an intimate and causal relationship between heterochromatin, nucleolar formation and the synthesis of ribonucleic acid in the cytoplasm of the cell.[9, 10] Broadly speaking, wherever cells undergo rapid protein synthesis, as in growth or secretory activity, there is usually an abundance of ribonucleic acid in the cytoplasm and prominent nucleoli in highly basophilic nuclei. In the toad this cytological and dynamic relationship stands out very clearly because the heterochromatin, which is the main source of the basophily in growing or secretory cells, is not inextricably mixed with the chromosomes but is segregated for the most part into discrete granules entirely removed from the chromosomes, and instead of one

or several nucleoli there are hundreds of them. Here each nucleolar complex consists of one or more heterochromatin granules, the main body of the nucleolus probably protein in nature,[9] and some ribonucleic acid the removal of which with ribonuclease does not morphologically affect the body of the nucleolus. It is clear that ribonucleic acid can be synthesized, or converted (from desoxy ribose) deep within the nucleus, and with the migration of the nucleoli to the nuclear wall and their absorption this is somehow transferred to the cytoplasm. But the localization of the heterochromatic granules initially on the inner wall of the nucleus, the invariable orientation of the granules towards the cytoplasm and the sequence of changes which occur at this site all suggest that most of the synthesis or conversion is occurring at the interface of the nucleus and cytoplasm where an abundance of surface energy is available.

Our observations show that the lampbrush chromosomes of the toad are normal and typical meiotic chromosomes in structure and behavior. This fact is stressed because earlier one of us (Painter[3]) postulated that lampbrush chromosomes were the result of some sort of reduplication process. Ordinarily, a great increase in nuclear volume is accompanied by the growth and division of the contained chromosomes, forming the giant chromosomes in the salivary glands of Diptera or highly polyploid nuclei as in the larval cells of many insects which grow by endomitosis. Koltzoff[8] thought that the side branches of lampbrush chromosomes represent reduplications of the primary "genonema" which are thrown off before polar spindle formation and which merge with the cytoplasm when the germinal vesicle breaks down. But since the granules which the side branches appear to enclose contain neither thymonucleic acid, as shown by Feulgen's stain, nor ribonucleic acid, as shown by Unna's stain, there is little to support this concept. On the other hand, with the increase in nuclear volume in the toad's egg there is a great increase in the amount of heterochromatin and in the number of nucleoli which form in association with the heterochromatic granules. If these nucleolar organizers are genetically the same as those which form nucleoli in ordinary somatic cells, then we may say that the germinal vesicle of the toad is highly polyploid in nucleolar organizers but otherwise lampbrush chromosomes are normal meiotic structures.

Perhaps the most important aspect of the present study is the striking demonstration that chromatin can exist and function within the nucleus apart from the chromosomes. And thus we are able to add another characteristic to the already long list of attributes of heterochromatin recently summarized by Darlington,[11] and the rôles this plays in the dynamic activities of cells.

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ON THE PERSEUS CLUSTER OF NEBULAE

BY F. ZWICKY

NORMAN BRIDGE LABORATORY OF PHYSICS, CALIFORNIA INSTITUTE OF TECHNOLOGY

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The Perseus cluster of nebulae (R.A. $3^h\ 15^m$, Dec. $+41°\ 15'$, 1930; gal. long. 118°, lat. $-13°$) according to Hubble and Humason[1] contains about 500 nebulae scattered over an area nearly 2° in diameter and lies at a distance of 11 million parsecs. As is the case with most clusters investigated, counts of nebulae made on photographs which were obtained with the 18-inch Schmidt telescope show that the Perseus cluster is considerably larger than was originally derived from the photographs taken with the large reflectors whose very severely restricted fields make them unsuitable for the efficient analysis of objects subtending large angles. For quite a different reason the analysis of the spatial distribution of the nebulae in the Perseus cluster with the 18-inch Schmidt telescope also presents considerable difficulties. The cluster is projected on a field of the Milky Way so rich in stars, that, because of the small scale of the telescope, the blurred images of close pairs and groups of stars may easily be mistaken for extragalactic nebulae. This error can partly be avoided by taking a number of well-focused photographs while the telescope is being drifted slightly in a different direction for each photograph. Groups of stars are likely to betray themselves by an image containing sharp streaks such as should not be expected in a drifted image of a nebula. Also, the precaution was taken to identify all of the nebulae involved several times through a repeated analysis conducted during several years and making use of many photographs taken on various emulsions. It is therefore felt that the results presented here can be viewed with more confidence than might have been originally hoped for.

In figure 1 the distribution of nebulae brighter than about the photographic magnitude $m_p = 16.5$ over a field of approximately 9° in diameter around the Perseus cluster is shown.

According to Hubble's investigations the Perseus cluster is seen through a large "window" of relatively high transparency in the galactic dust clouds. Lanes and pockets of heavy obscuration surround the cluster on the east, north and west sides. One dark pocket in which no nebulae and relatively few stars can be seen is marked *DP* in figure 1. The galactic plane lies in the dirction NNE about thirteen degrees from the center of the

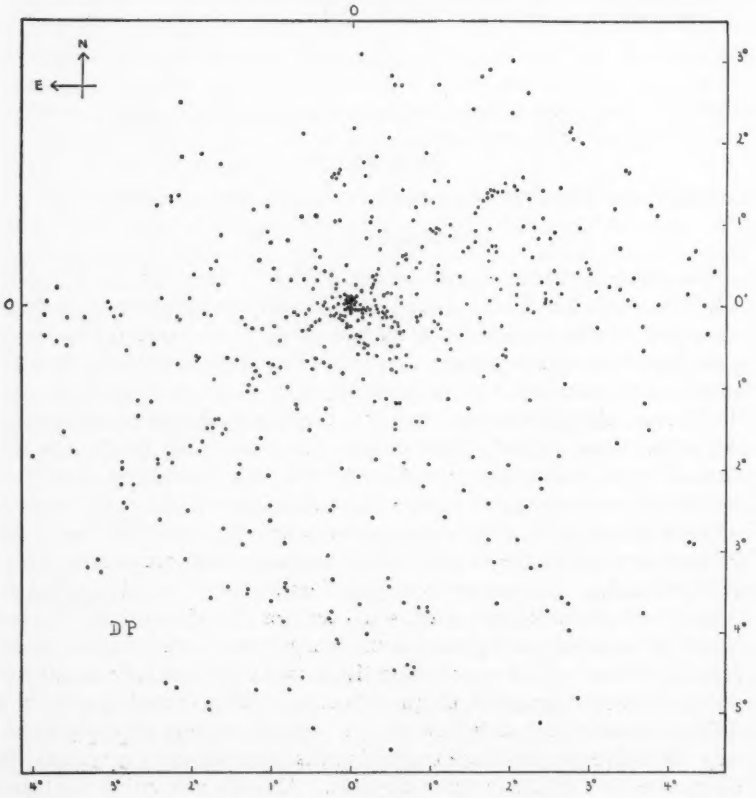

FIGURE 1
The Perseus cluster of nebulae.

cluster. Since in this direction at distances larger than five degrees the obscuration seems to increase rapidly, we have counted the nebulae in complete rings around the center of the Perseus cluster only to a radius of 200′ of arc. In table 1 are tabulated the total numbers n_r of nebulae contained in successive rings of 5′ of arc and 10′ of arc width, respectively. The last

TABLE 1

COUNTS OF NEBULAE IN THE PERSEUS CLUSTER IN RINGS WHOSE RADII DIFFER BY 5′ OF ARC AND 10′ ARC, RESPECTIVELY

NO. OF RING	QUADRANTS NE	NW	SW	SE	TOTAL n_r	N_r/SQ. DEG.
1	4	3	2	3	12	557
2	5	3	4	2	14	217
3	2	2	5	7	16	149
4	4	2	4	5	15	99
5	1	3	5	3	12	62
6	2	4	6	1	13	55
7	4	2	7	2	15	54
8	1	3	4	4	12	37
9	2	0	4	3	9	25
10	1	4	2	3	10	24.4
11–12	1	6	7	4	18	19.0
13–14	5	6	8	2	21	18.7
15–16	4	3	4	7	18	13.8
17–18	3	8	3	8	22	15.0
19–20	5	8	4	5	22	13.4
21–22	4	5	3	3	15	8.3
23–24	2	11	6	3	22	11.0
25–26	2	9	6	6	23	10.7
27–28	2	7	2	8	19	8.2
29–30	2	10	2	5	19	7.6
31–32	4	9	2	4	19	7.1
33–34	1	5	3	3	12	4.22
35–36	1	6	3	6	16	5.30
37–38	1	7	1	8	17	5.33
39–40	1	2	4	4	11	3.27
Total	64	128	101	109	402	
41–42	..	...	3	3	6	3.40
43–44	..	...	2	9	11	5.93
45–46	..	...	6	10	16	8.25
			SOUTH			
47–48			4		4	3.95
49–50			5		5	4.73
51–52			2		2	1.82
53–54			0		0	0.00
55–56			5		5	4.22
57–58			4		4	3.25
59–60			4		4	3.15
Total number of nebulae counted					459	

column gives the average numbers of nebulae N_r per square degree in these rings. The area inside of the first circle is 1/46.4 square degrees.

A total of 402 nebulae was counted within a radius of 200′ of arc from the center of the cluster. Within the fluctuations to be expected these nebulae

distribute themselves uniformly over the four quadrants, except that perhaps the NE quadrant shows a slight deficiency in the number of nebulae, which is presumably due to the increasing effects of obscuration on approaching the galactic plane. From the general appearance of the stellar field it seems safe to count nebulae in the SW and the SE quadrants to a distance of 230′ of arc and in the south quadrant bounded by the SW and SE directions to a distance of 300′ of arc and beyond from the center of the cluster. At a distance of about 250′ of arc south of the center the cluster nebulae here considered merge with the field nebulae which appear at an average density of about 3.0 nebulae per square degree. According to the counts presented here the Perseus cluster therefore has an angular diameter of at least 8° of arc and an actual diameter of at least 1.5×10^6 parsecs or five million light years.

According to Hubble[2] the average number N of nebulae per square degree in the general field is given by

$$\log_{10} N = 0.6 m_L - 9.1. \qquad (1)$$

In our case the limiting photographic magnitude m_L included in the counts is about $m_L = 16.5$. This according to equation (1) corresponds to $N = 6.3$ nebulae per square degree. From our observations we obtained $N' = 3.0$ nebulae per square degree instead, a result which according to (1) is equivalent to the average number over the unobscured parts of the sky of nebulae per square degree whose apparent photographic magnitude is smaller or equal to $m_L' = 15.95$. Since on Palomar Mountain the Perseus cluster can be observed within ten degrees of the zenith no appreciable zenith distance correction is to be introduced. If we therefore assume that the unobscured field of nebulae around the Perseus cluster is comparable to the average field of nebulae all over the unobscured parts of the sky we arrive at a value

$$\Delta m = m_L - m_L' = 0.55 \text{ magnitudes} \qquad (2)$$

for the local obscuration. This value is presumably smaller than the actual value because it is likely that the Perseus cluster is imbedded in the very large cloud of nebulae extending from Andromeda over Pisces into Perseus, a fact which would result in a local value for N larger than the average all over the sky and in a value for Δm larger than given by (2). Of the 460 nebulae counted about 360 nebulae are physical members of the Perseus cluster. Since these nebulae are all brighter than about the absolute magnitude $M = -14.3$ the total population of the Perseus cluster presumably includes well over one thousand nebulae.

[1] Hubble, E., and Humason, M. L., *Astrophys. Jour.*, **74**, 43 (1931).
[2] Hubble, E., *Ibid.*, **79**, 70 (1934).

A REVERSIBLE GROWTH INHIBITION OF ISOLATED TOMATO ROOTS*

BY JAMES BONNER

WILLIAM G. KERCKHOFF LABORATORIES, CALIFORNIA INSTITUTE OF TECHNOLOGY

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Introduction.—It is known that certain bacteria are inhibited in their growth by the presence of sulfanilamide or related compounds in the nutrient medium, and it has been suggested by Fildes[1] and by Woods[2] that this inhibition is due to specific interference with the utilization of essential metabolites, in particular *p*-amino benzoic acid. In the present paper data will be presented which show that the growth of isolated tomato roots[3] is inhibited in the presence of appropriate concentrations of sulfanilamide or its derivatives, but that this growth inhibition can be in whole or in part abolished by the further presence of *p*-amino benzoic acid, a substance not otherwise essential as a supplement for the growth of isolated tomato roots.

Methods.—Isolated tomato roots were cultured aseptically in the nutrient medium described earlier.[4] One centimeter tips from vigorously growing branch roots were used as inocula for the experimental cultures. Approximately 200 roots were grown in each experiment. The two hundred initial tips were randomly divided into 10 lots of 20 tips each and each treatment carried out on one or more lots. The conclusions contained in this paper are based on a series of 42 such experiments.

All cultures were maintained in Petri dishes, four roots per dish, in the dark at 25°C. for one week. At the end of this time the growth in length of the principal axis of each root was measured. The roots were then discarded and fresh inocula from stock cultures used in further experiments.

Three clones of roots, all of the variety "San Jose Canner"[5] were used. These clones, each of which had previously been subjected to 27 weekly transfers in the standard basal medium, reacted similarly to all of the treatments discussed below.

Experimental Results.—Table 1 shows that the growth of isolated tomato roots is inhibited by sulfanilamide and by sulfapyridine. In the presence of 30 mg. per liter of either of these substances isolated tomato roots grew only 15–21% as long in one week as similar roots not receiving inhibitor. Table 1 also shows that the growth inhibition caused by sulfanilamide or sulfapyridine is in part offset by the further addition of *p*-amino benzoic acid to the culture medium in the concentration of 1 mg. per liter. Roots receiving inhibitor and *p*-amino benzoic acid grew 3.3 to 4.5 times as much in one week as roots receiving inhibitor only. This effect cannot be ascribed to a general growth-promoting effect of *p*-amino benzoic acid, since, as shown in table 2, this substance in the concentration of 1 mg. per

liter is without effect on the growth of tomato roots. Increased (10 times) concentrations of nicotinic acid or pyridoxine did not affect the inhibition as did *p*-amino benzoic acid.

TABLE 1

THE EFFECT OF SULFANILAMIDE AND SULFAPYRIDINE ON THE GROWTH OF ISOLATED TOMATO ROOTS. GROWTH IN MM. PER ROOT PER WEEK

SUPPLEMENTS	SULFONILAMIDE EXPTS.	NO. OF ROOTS	MM./WEEK	SULFAPYRIDINE EXPTS.	NO. OF ROOTS	MM./WEEK
None	I–25	40	56.6 ± 2.2	I–24	38	45.0 ± 2.5
	I–31	26	49.8 ± 3.1	I–32	32	52.7 ± 1.6
30 mg. inhibitor/l.	I–25	33	12.0 ± 1.5	I–24	29	9.7 ± 1.3
	I–31	14	10.0 ± 1.3	I–32	30	7.8 ± 0.6
30 mg. inhibitor/l. + 1 mg. *p*-amino benzoic acid/l.	I–25	19	39.5 ± 3.4	I–24	17	37.9 ± 2.5
	I–31	16	36.2 ± 2.3	I–32	14	35.4 ± 1.4

TABLE 2

LACK OF EFFECT OF *p*-AMINO BENZOIC ACID ON THE GROWTH OF ISOLATED TOMATO ROOTS. GROWTH IN MM. PER ROOT PER WEEK

EXPTS.	NO *p*-AMINO BENZOIC ACID NO. OF ROOTS	LENGTH	1.0 MG./L. *p*-AMINO BENZOIC ACID NO. OF ROOTS	LENGTH
I–27	18	52.2 ± 4.3	18	53.6 ± 3.5
I–31	26	49.8 ± 3.1	16	49.1 ± 3.5
I–37	13	42.7 ± 1.8	17	41.8 ± 1.3

Sulfathiazole also inhibits the growth of isolated tomato roots as is shown in table 3, which gives the composite results of 16 experiments. Since the growth of untreated control roots varied from one experiment to the next (as in tables 1 and 2) the growth rates in each experiment were reduced to per cent of the untreated control growth rate and it is this relative growth rate which appears in table 3. It is clear from this table that

TABLE 3

INHIBITION OF THE GROWTH OF ISOLATED TOMATO ROOTS BY SULFATHIAZOLE AND ITS REVERSAL BY *p*-AMINO BENZOIC ACID. MEAN VALUES FROM 16 EXPERIMENTS. GROWTH RATES IN PER CENT OF CONTROL ROOTS GROWN FOR 1 WEEK IN STANDARD BASAL MEDIUM. THE AVERAGE GROWTH RATE (100%) OF THE CONTROL ROOTS WAS 45.8 ± 2.33 MM. PER WEEK IN THESE EXPERIMENTS

SULFATHIAZOLE CONC.; MG./L.	*p*-AMINO BENZOIC ACID CONCENTRATION; MG./L. GROWTH PER WEEK: % OF UNTREATED CONTROLS				
	0	0.03	0.10	0.30	1.0
100	3	...	...	...	27.5
30	15.2	17.0	21.0	25.0	53.6
10	18.4	20.0	32.3	58.7	94.6
3	37.4	52.2	83.0	99.0	100.7
1	67.6	92.3	97.7	99.0	...
0	100	...	...	...	100

sulfathiazole is a relatively potent inhibitor of root growth since half inhibition is given by about 2 mg. sulfathiazole per liter. The amount of *p*-amino benzoic acid needed to abolish a fixed amount of inhibition varies with the inhibitor concentration. Thus nearly the same absolute increase in growth rate was brought about by 0.03 mg. per liter of the material in the presence of 1 mg. per liter of sulfathiazole as was brought about by 1 mg. per liter of *p*-amino benzoic acid in the presence of 100 mg. per liter of sulfathiazole. Inhibition by a given quantity of sulfathiazole was markedly decreased by the addition of a 100 times smaller quantity of *p*-amino benzoic acid in every case. Inhibition by sulfathiazole and reversal of this inhibition by *p*-amino benzoic acid would seem to depend in part on the ratio between the two substances in the nutrient medium rather than strictly on the absolute amount of inhibitor present.

Isolated tomato roots of the clones used in these experiments appear, qualitatively, to contain *p*-amino benzoic acid or related substance of similar physiological activity,[6] even when grown through 40 or more successive weekly transfers in *p*-amino benzoic acid free medium. The presence of this material in such roots suggests that isolated tomato roots of the present clones may synthesize the substance.

Discussion.—The inhibition of the growth of isolated tomato roots by sulfathiazole depends in part on the ratio between added inhibitor and added *p*-amino benzoic acid. This observation might suggest that the inhibition is in part competitive in the sense that sulfathiazole may compete with *p*-amino benzoic acid for some essential position or function in the living cell. That sulfathiazole inhibits the growth of roots not supplied with *p*-amino benzoic acid is not in disagreement with this view since isolated tomato roots appear to normally contain this substance. Other factors may also govern the inhibition.[7]

Summary.—Isolated tomato roots of 3 different clones were found to be inhibited in growth by the addition of sulfanilamide, sulfapyridine or sulfathiazole, to the nutrient medium. This inhibition was in whole or in part abolished by the further addition of *p*-amino benzoic acid to the medium. Isolated tomato roots of the clones used normally contain *p*-amino benzoic acid, or a substance having similar physiological activity.

* Report of work done with the coöperation of the Work Projects Administration, O. P. No. 165-1-07-172. This work was made possible in part by the support of Merck and Company.

[1] Fildes, P., *British Jour. Expt. Path.*, **21**, 67 (1940).

[2] Woods, D. D., *Ibid.*, **21**, 74 (1940).

[3] White, P. R., *Plant Physiology*, **9**, 585 (1934). Robbins, W. J., and Bartley, Mary, *Science*, **85**, 246 (1937).

[4] Bonner, J., *Amer. Jour. Bot.*, **27**, 692 (1940). This medium contains per liter of redistilled water: 1.5 mg. ferric tartrate, 20 mg. KH_2PO_4, 65 mg. KCl, 81 mg. KNO_3, 36 mg. $MgSO_4 \cdot 7H_2O$, 236 mg. $Ca(NO_3)_2 \cdot 4H_2O$, and 20 gm. sucrose.

[5] The seed used was kindly supplied by the California Packing Corporation.

[6] The assays for *p*-amino benzoic acid were carried out by Prof. G. W. Beadle and Prof. E. Tatum, Stanford University, using a mutant of *Neurospora crassa* for which *p*-amino benzoic acid is an essential supplement.

[7] In 5 experiments sulfanilamide or its derivatives were applied to intact tomato plants grown in the greenhouse in sand or solution culture. Concentrations of up to 125 mg. per liter of nutrient were found to be without marked inhibiting effect on root or top growth.

GENERAL CONGRUENCES INVOLVING THE BERNOULLI NUMBERS

BY H. S. VANDIVER

DEPARTMENT OF PURE MATHEMATICS, THE UNIVERSITY OF TEXAS

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Kummer[1] gave a result which may be expressed as follows:

$$h^n(h^{p-1} - 1)^i \equiv 0 \pmod{p^i}, \ (n - 1 \geqq i;\ n \not\equiv 0 \pmod{\overline{p - 1}}), \quad (1)$$

where p is an odd prime; the left-hand member is expanded in full, then b_t/t is substituted for h^t, and the b's are defined by the recursion formula

$$(b + 1)^n = b_n, \quad (n > 1),$$

in which we expand the left-hand member by the binomial theorem and substitute b_k for b^k. The latter formula gives the Bernoulli numbers. The congruences (1) have played an important part in the development of the arithmetic theory of these numbers.

In the present paper we shall employ the theorem which the writer gave in another paper,[2] the statement of which, for convenience, is repeated here:

THEOREM I. *Let R be the ring of algebraic integers in an algebraic field and put*

$$f_{n_i}^{(i)}(\alpha_1, \alpha_2, \ldots, \alpha_{k_i}) = \sum_{r=1}^{k_i} \alpha_{ri} a_{ri}^{n_i} \quad (2)$$

where the a's and α's are in R and the n's are rational integers $\geqq 0$. Further let there be a rational integer $d > 0$ such that for all r's in the range 1 to k_i and all i's in the range 1 to s,

$$a_{ri}^{\,d} \equiv 1 \pmod{\mathfrak{m}} \quad (3)$$

where $\mathfrak{m}$ is a fixed ideal in R. Also, let

$$\beta_1 + \beta_2 + \ldots + \beta_s \equiv 0 \pmod{\mathfrak{m}}$$

where the β's are in R and suppose that $\mathfrak{a}_i$ is the greatest common ideal divisor of the ideals.

$$(a_{ri}),\ r = 1, 2, \ldots, k_i,$$

each of which has a factor, $\neq (1)$ in common with $\mathfrak{m}$, then

$$(f_{n_1} + f_{n_2} + \ldots + f_{n_s})^j \equiv 0(\text{mod } (\mathfrak{m}^j, \mathfrak{a}_1, \mathfrak{a}_2, \ldots, \mathfrak{a}_s)) \qquad (4)$$

where we expand the left-hand member in full and set

$$f_{ni}{}^j = \beta^j f_{n_i + id}{}^{(i)}(\alpha_1, \alpha_2, \ldots, \alpha_{ki}),$$
$$j = 1, 2, \ldots, s.$$

We shall now obtain wide generalizations of (1). In another article the writer defined what was called a Bernoulli number of the rth order as follows:

$$(m_r b^{(r)} + m_{r-1} b^{(r-1)} + \ldots + m_1 b' + m_0)^n \qquad (5)$$
$$= b_n(m_r, m_{r-1}, \ldots, m_0)$$
$$m_i \neq 0,\ (i = 1, 2, \ldots, r),$$

where the left-hand member is expanded in full and b_s substituted for

$$b_s{}^{(k)};\ k = 1, 2, \ldots, r.$$

For $r = 1$ and 2, it will be shown that congruences of the type (1) as well as much more general ones also hold for these Bernoulli numbers of higher order. We then use methods which will apply to other formulae involving generalized Bernoulli numbers as well as congruences. They consist in the main of obtaining congruences involving (5) for $r = 1$ and 2 and then noting that the relations hold for each positive integral value of m. It is then possible to eliminate the m's and obtain entirely new types of formulae involving the ordinary Bernoulli numbers and binomial coefficients only.[3] An example of this depends on the congruence,[4] modulo p,

$$t_n(m, k) \equiv \sum_{\rho}{}' \frac{(-1)^{n+1}\rho^k f_{n-1}(\rho)}{1 - \rho^p} + \sum_{l=0}^{k-1} \sum_{\rho} l^{n-1}\rho^{l-k} \qquad (6)$$

where

$$\frac{(mb + k)^n - b_n}{n} = t_n(m, k),$$

and

$$f_a(x) \equiv 0^a + x + 2^a x^2 + \ldots + (p-1)^a x^{p-1},$$

with

$$0^\circ = 1,\ p \text{ is prime},\ (m, p) = 1,\ m > 1$$

and

$$\sum_\rho', \sum_\rho$$

the first symbol meaning that summation is to be taken over all the distinct mth roots of unity except unity, and the second symbol meaning summation over all the distinct mth roots of unity. Each one of the terms in the right-hand members of (6) may be put in the form (2); hence we may apply Theorem I, and obtain, if the β's are rational integers and p is a rational prime,

$$\begin{gathered} t_1^{n_1} t_2^{n_2} \ldots t_s^{n_s} (\beta_1 t_1^{p-1} + \beta_2 t_2^{p-1} + \ldots + \beta_s t_s^{p-1}) \qquad (7) \\ \equiv 0 (\text{mod } p^j,\ p^{n_1 - 1},\ p^{n_2 - 1},\ \ldots,\ p^{n_s - 1}) \\ n_i \not\equiv 0 (\text{mod } p - 1);\ i = 1, 2, \ldots, s, \\ \beta_1 + \beta_2 + \ldots + \beta_s \equiv 0 (\text{mod } p) \end{gathered}$$

where the left-hand member is expanded in full and $t_i(m, k)$ substituted for t_c^i; $c = 1, 2, \ldots s$. In another article[5] I gave a result which may be obtained from (7) by putting $k = 0$ and noting that we can take n so that

$$n^{p-1} \equiv 1 (\text{mod } p^j). \qquad (7a)$$

The relation (7) is only one of a number of relations of this general type which may be obtained from (4); we may, for example, take any of the f's in (4) as being unity. Also from (4) we may obtain relations similar to (7) but with the β's integers in an algebraic field R and instead of p we have a prime ideal P in R, with also $(N(P) - 1)$ replacing $(p - 1)$ in the exponents appearing in the left-hand member of (7), if $N(P)$ represents the norm of P in R.

In particular from (7) we find, for $n \not\equiv 0 \pmod{(p-1)}$,

$$t^n (t^{p-1} - 1)^j \equiv 0 (\text{mod } p^j,\ p^{n-1})$$

from which we obtain, after employing

$$h^n (h^{p-1} - 1)^j \equiv 0 (\text{mod } p^j,\ p^{n-1}),$$

$$\sum_{i=0}^{j} (-1)^i \frac{(mb + k)^{n + i(p-1)}}{n + i(p-1)} \binom{j}{i} \equiv 0 (\text{mod } p^j, p^{n-1}) \qquad (8)$$

In this we may set $k = 1$ and let m belong to the exponent r, modulo p^j,

with $r \leqq p - 1$, then by setting $m, m^2, \ldots, m^r$ in turn we obtain a set of congruences from which we may eliminate m and obtain, if $c < r$,

$$\sum_{k=0}^{a} \sum_{i=0}^{j} (-1)^i \binom{j}{i} \binom{n + i(p-1)}{c + kr} \frac{b_{c+kr}}{n + i(p-1)} \equiv 0 \pmod{(p^j, p^{n-1})} \tag{9}$$

$$a = \left[\frac{s - c}{r}\right]; \quad s = n + i(p - 1).$$

This obviously differs from (1) in a number of ways, for example, the subscripts of the b's ascend by multiples of r (a divisor of $(p - 1)$) instead of multiples of $(p - 1)$. Now set $B_n = (-1)^{n-1} b_{2n}$; $n > 1$ and $B_0 = 1$.

In another article[6] the writer discussed the concept of regular primes. First, an improper divisor of a Bernoulli number is defined as a prime number p such that $B_n \equiv 0 \pmod{p}$, with also $n \equiv 0 \pmod{p}$. A proper divisor p of B_n is such that $B_n \equiv 0 \pmod{p}$ with $(n, p) = 1$. From the relation, if $n \not\equiv 0 \pmod{(p - 1)}$,

$$\frac{b_n}{n} \equiv \frac{b_{n+p-1}}{n + p - 1} \pmod{p}$$

it is easy to show that a regular prime is not a proper divisor of any Bernoulli number but an irregular prime is a proper divisor of an infinity of Bernoulli numbers, if we define a regular prime as one that divides at least one of the Bernoulli numbers B_n; $n = 1, 2, 3, \ldots (p - 3)/2$. *This provides then a separation of primes into two classes.* It is possible to extend all of these notions to numbers of the type $(mb + k)^n$. To provide a straight generalization of the notion of regular prime we may first restrict ourselves to n even. Elsewhere[7] the writer proved that if $n = n_1 p$, $n_1 \not\equiv 0 \pmod{p - 1}$, $(m, p) = 1$, then $(mb + k)^n \equiv 0 \pmod{p}$, where m and k are integers, p prime. In view of this relation we may generalize directly the concepts of regular and irregular primes, and also proper and improper divisors. If none of the numbers $(mb + k)^{2n}$; with $n = 1, 2, \ldots, (p - 3)/2$ is divisible by p we say that p is (m, k) regular; otherwise it is termed (m, k) irregular. In view of the result just quoted, it is easy to show that, employing (8) for $j = 1$ that a prime which is (m, k) regular is not a proper divisor of any generalized Bernoulli number of the first order defined by m and k, whereas, an (m, k) irregular prime is the proper divisor of an infinity of (m, k) Bernoulli numbers. In view of this, corresponding to each integral value of m excepting $m = 0$ and each integral value of k, there is a separation of the rational primes into two classes. We may obviously extend the notion of (m, k) regular primes to the case where n is odd and less than $p - 1$. Primes which do not divide any of the $(mb + k)^n$; $n = 1, 2, \ldots,$

$p - 2$, will be referred to as strongly (m, k) regular. Such primes exist; it will be found that 5 is a (3, 1) strongly regular prime and 7 is a strongly (3, 2) regular prime. Elsewhere[8] the writer proved the congruence theorem concerning ordinary Bernoulli numbers. This theorem also holds if we replace the ordinary Bernoulli numbers by any Bernoulli numbers of the first or second order. Then, by the method indicated in the present paper, we can obtain new relations involving the ordinary Bernoulli numbers. If we employ the relation (5) on page 199 of a paper[4] previously referred to, together with (7a) of the present paper, we obtain, on the elimination of m, and k, congruences analogous to (9) but involving products of two Bernoulli numbers in each term.

[1] *Journal für Mathematik*, **41**, 368, 372 (1851).

[2] These PROCEEDINGS, **28**, 26–27 (1942).

[3] In another article the writer obtained certain *equations* involving the ordinary Bernoulli numbers by employing initially the generalized Bernoulli numbers. Cf. *Duke Math. Jour.*, **8**, 582 (1941).

[4] These PROCEEDINGS, **25**, 200 (1939).

[5] *Bull. Amer. Math. Soc.*, **43**, 422 (1937).

[6] These PROCEEDINGS, **18**, 594–597 (1932).

[7] *Duke Math. Jour.*, **8**, 580 (1941).

[8] *Bull. Amer. Math. Soc.*, **46**, 121 (1940), Theorem I.

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*TRANSFORMATION THEORY OF ISOGONAL TRAJECTORIES OF ISOTHERMAL FAMILIES**

BY EDWARD KASNER AND JOHN DE CICCO

DEPARTMENTS OF MATHEMATICS, COLUMBIA UNIVERSITY AND ILLINOIS INSTITUTE OF TECHNOLOGY

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1. Isothermal Transformations.—It is known that the conformal transformations are the only *point* correspondences of the plane which convert all isothermal families of curves into isothermal families.

Kasner's extension of this result is that the total group of *lineal-element* transformations which send all isothermal families into isothermal families is given in cartesian coördinates $(x, y, \theta = \text{arc tan } dy/dx)$ by

$$X = \phi(x, y), \pm Y = \psi(x, y), \Theta = a\theta + h(x, y), \qquad (1)$$

where $\phi + i\psi$ is a monogenic function of $z = x + iy$, h is any harmonic function of (x, y), and a is a non-zero constant. The contact part is merely the conformal group.[1]

This is a generalization to transformations of first order differential

elements. In our new work, we shall extend this result to transformations of curvature-elements, that is, second order differential elements.[2]

2. The Complete System Γ_0 of the Isogonal Trajectories of an Isothermal Family.—To accomplish the purpose stated above, we find that the appropriate geometric object to be studied is the system Γ_0 of all the isogonal trajectories of an isothermal family. If k represents the curvature, the differential equation of any such system Γ_0 may be written as

$$k = \lambda(x, y) \sin \theta + \mu(x, y) \cos \theta, \tag{2}$$

where $\lambda + i\mu$ is a monogenic function of z.

Any Γ_0 system is conformally equivalent to the ∞^2 straight lines of the plane. Thus our system Γ_0 may be briefly defined as a *conformal rectilinear wex.*[3]

Various properties of Γ_0 systems may be mentioned.[4] The complete set of isogonal trajectories of a family of curves is a linear system if and only if the set is a Γ_0 system. The Γ_0 systems are the only sets which are both natural and isogonal. The associated point correspondence of a Γ_0 system is direct conformal. The reciprocal (conjugate) of a Γ_0 system is also a Γ_0 system.

3. Fundamental Theorem.—The complete group of curvature-element-transformations which send any system Γ_0 of all the isogonal trajectories of an isothermal family into another such system Γ_0 is given in cartesian coördinates (x, y, θ, k) by

$$X = \phi(x, y), \pm Y = \psi(x, y), \pm \Theta = \theta + \arctan \frac{\beta(x, y)}{\alpha(x, y)},$$

$$K = (\alpha^2 + \beta^2)^{-1/2} [k + \gamma(x, y) \sin \theta + \delta(x, y) \cos \theta], \tag{3}$$

where $\phi + i\psi$, $\alpha + i\beta$, $\gamma + i\delta$ are all monogenic functions of $z = x + iy$ only. (Either both upper or both lower signs are taken.)[5]

A corollary of our theorem is that the only contact transformations of curvature-elements preserving the class of all Γ_0 systems are the conformal ones.

4. Proof of Our Fundamental Theorem.—For proof, we employ the following minimal coördinates:

$$u = x + iy, v = x - iy, p = \frac{dv}{du} = e^{-2i\theta}, q = \frac{d^2v}{du^2} \Big/ \frac{dv}{du} = 2ikp^{1/2}. \tag{4}$$

Thus any curvature-element is given by (u, v, p, q).

Any Γ_0 system is then given by the equation

$$q = c(u) + pd(v). \tag{5}$$

Thus any second order differential equation $q = q(u, v, p)$ represents a Γ_0 system if and only if

$$q_{pp} = 0,\ q_{up} = 0,\ pq_{vp} = q_v,\ q_{uv} = 0. \tag{6}$$

Consider now the general curvature-element transformations

$$U = U(u, v, p, q),\ V = V(u, v, p, q),\ P = P(u, v, p, q),\ Q = Q(u, v, p, q), \tag{7}$$

with non-vanishing jacobian J. We shall find all such transformations which preserve the class of Γ_0 systems.

Let q defined by (5) be placed into (7). Then Q becomes a function of (U, V, P). We find

$$\frac{\partial Q}{\partial P} = \frac{\alpha + \beta q_u + \gamma q_v + \delta q_p}{a + bq_u + cq_v + dq_p} \tag{8}$$

where

$$a = \begin{vmatrix} U_u U_v U_p \\ V_u V_v V_p \\ P_u P_v P_p \end{vmatrix},\ b = \begin{vmatrix} U_q U_v U_p \\ V_q V_v V_p \\ P_q P_v P_p \end{vmatrix},\ c = \begin{vmatrix} U_u U_q U_p \\ V_u V_q V_p \\ P_u P_q P_p \end{vmatrix},\ d = \begin{vmatrix} U_u U_v U_q \\ V_u V_v V_q \\ P_u P_v P_q \end{vmatrix}, \tag{9}$$

and where $\alpha, \beta, \gamma, \delta$ are obtained from a, b, c, d, respectively, by replacing P by Q.

Next let A and B denote the expressions

$$\begin{aligned} A &= (a\beta - b\alpha) + q_v(c\beta - b\gamma) + q_p(d\beta - b\delta), \\ B &= (a\gamma - c\alpha) + q_u(b\gamma - c\beta) + q_p(d\gamma - c\delta). \end{aligned} \tag{10}$$

Now upon setting $\partial^2 Q/\partial P^2 = 0$, and taking account of the conditions $q_{pp} = q_{up} = 0$, $q_{vp} = q_v/p$, we find that for arbitrary Γ_0 systems, the partial derivatives q_{uu} and q_{vv} will be effectively present in $\partial^2 Q/\partial P^2$ unless their coefficients vanish. Hence these must be zero, and we find

$$\begin{aligned} A[(U_v V_p - U_p V_v) + q_v(U_q V_p - U_p V_q) + q_p(U_v V_q - U_q V_v)] &= 0, \\ B[(U_u V_p - U_p V_v) + q_u(U_q V_p - U_p V_q) + q_p(U_u V_q - U_q V_u)] &= 0. \end{aligned} \tag{11}$$

Since $\partial^2 Q/\partial U \partial P = 0$, there are equations similar to the above where U is replaced by P. Also since $P\partial^2 Q/\partial V \partial P = \partial Q/\partial V$, there are another set of equations similar to the above where V is replaced by P.

We shall prove first that $A = B = 0$. For if $A \neq 0$, then by (11) and similar equations, it can be shown that if at least one of the quantities $U_p, U_q, V_p, V_q, P_p, P_q$ is not zero, then $U_v : U_p : U_q = V_v : V_p : V_q = P_v : P_p : P_q$. This makes the jacobian vanish. The other possibility, $U_p = U_q = V_p = V_q = P_p = P_q = 0$, also makes the jacobian zero. Hence $A \neq 0$ leads to a contradiction. A similar argument will prove $B = 0$.

Next we shall show that $b = c = \beta = \gamma = 0$. Since $A = B = 0$, it follows from (10) that

$$a\beta - b\alpha = a\gamma - c\alpha = b\gamma - c\beta = b\delta - d\beta = c\delta - d\gamma = 0. \quad (12)$$

Now if at least one of the quantities b, c, β, γ is not zero, then $a:b:c:d = \alpha:\beta:\gamma:\delta$. This makes the jacobian zero. Therefore $b = c = \beta = \gamma = 0$.

Now we shall prove that $U_pV_q - U_qV_p = 0$. For otherwise from (9), we discover since $b = c = 0$ that P is a function of U and V only. This is impossible.

Therefore our required transformations must necessarily satisfy the following equations

$$\begin{gathered} U_pV_q - U_qV_p = 0, \\ P_p(U_pV_q - U_qV_v) + P_q(U_pV_v - U_vV_p) = 0, \\ P_p(U_uV_q - U_qV_u) + P_q(U_pV_u - U_uV_p) = 0, \end{gathered} \quad (13)$$

and similar equations where P is replaced by Q.

We shall show next that $U_q = V_q = 0$. For otherwise if $U_q \neq 0$, it follows from the preceding equations that

$$\begin{gathered} V_q = \rho U_q,\ V_p = \rho U_p, \\ (V_v - \rho U_v)(U_pP_q - U_qP_p) = (V_u - \rho U_u)(U_pP_q - U_qP_p) = 0. \end{gathered} \quad (14)$$

Now if $U_pP_q - U_qP_p \neq 0$, then V is a function of U only. Since this is obviously impossible, the other possibility is $U_pP_q - U_qP_p = 0$. From this, the preceding equations, and similar equations where P is replaced by Q, we find that $U_p:U_q = V_p:V_q = P_p:P_q = Q_p:Q_q$. This makes the jacobian vanish. Hence $U_q = 0$. By a similar argument $V_q = 0$.

The equations $b = c = \beta = \gamma = 0$ now become since P_q or $Q_q \neq 0$

$$U_vV_p - U_pV_v = U_uV_p - U_pV_u = 0. \quad (15)$$

If U_p or $V_p \neq 0$, then $U_u:V_u = U_v:V_v = U_p:V_p$. This is impossible. Hence *in all cases* $U_p = V_p = 0$.

Therefore our required transformations must *necessarily* be of the form

$$U = U(u, v),\ V = V(u, v),\ P = P(u, v, p, q),\ Q = Q(u, v, p, q). \quad (16)$$

If this transformation is to convert any Γ_0 system into a Γ_0 system, then geometrically we observe that, for any fixed point (u, v) and the corresponding fixed point (U, V), a linear equation in (p, q) must be carried into a linear equation in (P, Q). Therefore P and Q must necessarily be given by

$$P = \frac{a_2p + b_2q + c_2}{a_1p + b_1q + c_1}, \qquad Q = \frac{a_3p + b_3q + c_3}{a_1p + b_1q + c_1}, \quad (17)$$

where (a_j, b_j, c_j) are functions of (u, v) only.

If $q = c + dp$ becomes $Q = C + DP$, then

$$\begin{aligned} c(b_1C + b_2D - b_3) + (c_1C + c_2D - c_3) &= 0, \\ d(b_1C + b_2D - b_3) + (a_1C + a_2D - a_3) &= 0. \end{aligned} \tag{18}$$

Differentiating the top equation with respect to v, and the bottom equation with respect to u, we find

$$c\left[C\frac{\partial b_1}{\partial v} + D\frac{\partial b_2}{\partial v} - \frac{\partial b_3}{\partial v} + b_1C_UU_v + b_2D_VV_v\right] + \left[C\frac{\partial c_1}{\partial v} + D\frac{\partial c_2}{\partial v} - \frac{\partial c_3}{\partial v} + c_1C_UU_v + c_2D_VV_v\right] = 0, \tag{19}$$

$$d\left[C\frac{\partial b_1}{\partial u} + D\frac{\partial b_2}{\partial u} - \frac{\partial b_3}{\partial u} + b_1C_UU_u + b_2D_VV_u\right] + \left[C\frac{\partial a_1}{\partial u} + D\frac{\partial a_2}{\partial u} - \frac{\partial a_3}{\partial u} + a_1C_UU_u + a_2D_VV_u\right] = 0.$$

Since these equations are true for all values of C_U and D_V, we obtain

$$\begin{aligned} U_v(cb_1 + c_1) &= 0, \qquad V_v(cb_2 + c_2) = 0, \\ U_u(db_1 + a_1) &= 0, \qquad V_u(db_2 + a_2) = 0. \end{aligned} \tag{20}$$

If $U_uU_v \neq 0$ or $V_uV_v \neq 0$, the transformation becomes singular. Hence we have either one of the two cases

$$\begin{aligned} A&: \quad U = \phi(u), \qquad V = \psi(v); \\ B&: \quad U = \phi(v), \qquad V = \psi(u). \end{aligned} \tag{21}$$

Substituting case A into (19) and (20), we find after some manipulation the transformation

$$\begin{aligned} &U = \phi(u),\ V = \psi(v),\ P = \frac{\alpha_2(v)p}{\gamma_1(u)}, \\ &Q = \frac{1}{\gamma_1(u)}\left[q + \alpha_3(v)p + \gamma_3(u)\right]; \end{aligned} \tag{22}$$

whereas substituting case B into (19) and (20), we discover

$$\begin{aligned} &U = \phi(v),\ V = \psi(u),\ P = \frac{\gamma_2(u)}{\alpha_1(v)p}, \\ &Q = \frac{1}{\alpha_1(v)p}\left[q + \alpha_3(v)p + \gamma_3(u)\right]. \end{aligned} \tag{23}$$

Putting these into cartesian coördinates, we finally find our fundamental theorem.

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[1] Kasner, "Lineal Element Transformations Which Preserve the Isothermal Character," *Proc. Nat. Acad. Sci.*, **27**, 406–409 (1941).

Kasner, "Transformation Theory of Isothermal Families and Certain Related Trajectories," *Revista de Matematica*, **2**, 17–24 (1941).

De Cicco, "The Two Conformal Covariants of a Field," *Revista de Matematica*, **2**, 59–66 (1941).

[2] A generalization of Kasner's theorem has already been given in another direction. This other work is concerned with *field-element* to *lineal-element* transformations. See Kasner and De Cicco, "Generalized Transformation Theory of Isothermal and Dual Families," *Proc. Nat. Acad. Sci.*, **28**, 52–55 (1942).

[3] The word *wex* was introduced by Kasner to denote any doubly-infinite system of plane curves. It is therefore represented by a general differential equation of second order $y'' = f(x, y, y')$.

[4] See Kasner, *Princeton Colloquium Lectures*, 1912, 1934. Also Kasner, "Isothermal Systems in Dynamics," *Bull. Am. Math. Soc.*, **14**, 169–172 (1908); and "A Characteristic Property of Isothermal Systems of Curves," *Mathematische Annalen*, **59**, 352–354 (1904).

[5] The content of our new group is expressed by the symbol $2\infty^{6f(1)}$, whereas the content of Kasner's group, equations (1), is $2\infty^{1+4f(1)}$. See Kasner, "A Notation for Infinite Manifolds," *Am. Math. Monthly*, **49**, 243–244 (1942).

DIFFERENTIAL EQUATIONS OF THE TYPE: $y''' = Gy'' + Hy''^2$*

BY EDWARD KASNER

DEPARTMENT OF MATHEMATICS, COLUMBIA UNIVERSITY

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1. Differential Equations of the Type G.—The purpose of the present article is to discuss the various problems in geometry and especially physics which give rise to the general third order differential equations of the type

$$y''' = G(x, y, y')y'' + H(x, y, y')y''^2. \qquad (G)$$

Any such differential equation, or the system of its ∞^3 integral curves will be said to be of *the type G*. In our previous work, we referred to such systems as those possessing *the Property I*.

These differential equations of type G were first met in the investigation of dynamical trajectories in general positional fields of force. We shall briefly consider in connection with the differential equations of the type G the following topics: (1) The ∞^3 trajectories of a given field of force, (2) the complete system of velocity curves, (3) the systems S_k, (4) the general catenaries, (5) the ∞^3 brachistochrones in a conservative field, (6) sectional families, (7) curvature trajectories and (8) additive-multiplicative trajectories. All these species of (G), except (8), are projectively invariant.

2. Geometric Properties of Any System of Curves of the Type G.—Let us

consider any set of ∞^3 curves given by the general differential equation of the third order

$$F: \quad y''' = f(x, y, y', y'').$$

Through any lineal element E, there pass ∞^1 curves of our family F. To these curves at E, construct the osculating parabolas (all those which have four-point contact with the curves at E). The following two geometrically equivalent properties, which we call Property I, distinguish all systems of curves of the type G among all families F.

(I_a). *The foci of the* ∞^1 *osculating parabolas, constructed at the lineal element E, describe a circle passing through the point of E.*

(I_b). *The directrices of these parabolas form a pencil of straight lines.*

In a recent article,[2] Terracini gave the following elegant characterization of the type G by conic sections. Consider the family F and let C be any curve of F containing the lineal element E. At E, construct all the conic sections which have four-point contact with (that is, the same curvature, and the same rate of variation of curvature as) C at E. For the single curve C, there are ∞^1 such conics. Since ∞^1 curves C of the family F pass through E, there are in all ∞^2 conic sections. Terracini's theorem, which is essentially equivalent to our Property I, is:

The ∞^2 *conic sections corresponding to any lineal element E form a linear family.*

This result illustrates the projective character of the differential equations of the type G. It may be proved[1] that *the complete group of contact transformations preserving the class of differential equations of the type G is the projective group consisting of collineations and correlations.* However, the geometry of dynamical trajectories belongs to the group of collineations and not to the total projective group.

3. Trajectories in an Arbitrary Field of Force.—Consider the motion of a particle of unit mass in the plane under the action of any positional field of force. The equations of motion are

$$\frac{d^2x}{dt^2} = \phi(x, y), \quad \frac{d^2y}{dt^2} = \psi(x, y), \tag{1}$$

where ϕ and ψ are the rectangular components of the force acting at any point (x, y). We omit the trivial case of zero force.

If a particle is started from any position (x_0, y_0) with any velocity $(dx_0/dt_0, dy_0/dt_0)$, a definite trajectory is described. Since the same curve may be obtained by starting from any one of its ∞^1 points, the total number of trajectories, for all initial conditions, is ∞^3. By eliminating the time t from (1), the differential equation of the third order representing this system of trajectories is found to be of the type G where

$$G = \frac{\psi_x + (\psi_y - \phi_x)y' - \phi_y y'^2}{\psi - y'\phi}, H = -\frac{3\phi}{\psi - y'\phi}. \quad (2)$$

The complete geometric characterization of the ∞^3 trajectories of a given positional field of force has been given in our preceding work (see reference 1).

4. General Velocity Systems.—As stated above, if the initial position and the initial velocity of a particle of unit mass are given, the motion is determined. However, if only the initial position and the direction of motion are given, the radius of curvature r will depend for its value on the initial speed v. Therefore in addition to the usual formula $v^2 = (dx/dt)^2 + (dy/dt)^2$, there must be a formula expressing v^2 in terms of x, y, y', r. This is furnished by the familar equation

$$v^2 = rN, \quad (3)$$

where N denotes the principal normal component of the force, so that

$$N = \frac{\psi - y'\phi}{(1 + y'^2)^{1/2}}. \quad (4)$$

The equation (3) may then be written as

$$v^2 = \frac{(\psi - y'\phi)(1 + y'^2)}{y''}. \quad (5)$$

In the actual trajectory v varies from point to point. If now we replace v^2 in this result by some constant, say $1/c$, the resulting equation may be written as

$$y'' = c(\psi - y'\phi)(1 + y'^2). \quad (6)$$

The curves satisfying this differential equation (they are not in general trajectories) we define as *velocity curves*. For any field, a curve is a velocity curve corresponding to the speed v_0, provided a particle starting from any lineal element of the curve with that speed describes a trajectory osculating the curve.

In a given field of force, there are ∞^3 trajectories and ∞^3 velocity curves. The complete system of velocity curves is represented by a differential equation of the type G where

$$G = \frac{\psi_x + y'(\psi_y - \phi_x) - y'^2\phi_y}{\psi - y'\phi}, H = -\frac{\phi}{\psi - y'\phi} + \frac{2y'}{1 + y'^2}. \quad (7)$$

For a given value of c, there are ∞^3 velocity curves. The study of such sets of ∞^2 velocity curves is related to *conformal* geometry,[3] while the totality of ∞^3 curves is essentially *projective*.

5. The Systems S_k.—For a given positional field of force, we have thus far discussed the triply-infinite systems of trajectories and velocity curves. Other noteworthy systems of curves are connected with a field, for example brachistochrones, catenaries and tautochrones. Omitting the tautochrones, *the other systems named may all be obtained as special cases of this simple general problem:* to find curves along which a constrained motion is possible such that the pressure is proportional to the normal component of the force.

If an arbitrary curve is drawn in the plane field of force, and a particle of unit mass is started along it from one of its points with a given speed, the constrained motion along the given curve is determined. The acceleration along the curve is given by T, the tangential component of the force vector. So the speed at any point is

$$v^2 = 2\int T ds. \tag{8}$$

The pressure P (of course, normal to the curve) is

$$P = \frac{v^2}{r} - N. \tag{9}$$

The general problem suggested is to find curves such that P shall be proportional to N. So $P = kN$. To a given value of k, there correspond ∞^3 such curves: the system so obtained will be denoted by S_k. The four special cases of physical interest are:

$k = 0$ gives S_0, the system of *trajectories;*
$k = -2$ gives S_{-2}, the system of *brachistochrones;*
$k = 1$ gives S_1, the system of *catenaries;*
$k = \infty$ gives S_∞, the system of *velocity curves.*

The differential equation of the system, in intrinsic form, is easily obtained by eliminating v from the equations

$$v^2 = (k+1)rN,\ vv_s = T. \tag{10}$$

The result is

$$Nr_s = {}_nT - rN_s, \tag{11}$$

where $n = 2/(k+1)$.

Placing this into cartesian coördinates, we find that the differential equation of any system S_k is of the type G where

$$G = \frac{\psi_x + (\psi_y - \phi_x)y' - \phi_y y'^2}{\psi - y'\phi},\ H = -\frac{3\phi}{\psi - y'\phi} - \frac{(n-2)(\phi + y'\psi)}{(1+y'^2)(\psi - y'\phi)}. \tag{12}$$

Complete geometric characterizations of the system S_k have been given (see reference 1).

6. *Sectional Families.*—Now we shall discuss our first purely geometric problem. A *sectional family* of curves is defined by taking all the ∞^3 plane sections of an arbitrary surface and projecting them from some fixed center on to a fixed plane.[4]

Let $z = \phi(x, y)$ be an arbitrary surface in space. The orthogonal projections of the ∞^3 plane sections of this surface upon the xy-plane are given in the finite form by

$$ax + by + c\phi(x, y) + d = 0. \tag{13}$$

Eliminating the arbitrary constants a, b, c, d, we find that the sectional family is given by a differential equation of the type G where

$$G = \frac{\phi_{xxx} + 3y'\phi_{xxy} + 3y'^2\phi_{xyy} + y'^2\phi_{yyy}}{\phi_{xx} + 2y'\phi_{xy} + y'^2\phi_{yy}}, H = \frac{3\phi_{xy} + 3y'\phi_{yy}}{\phi_{xx} + 2y'\phi_{xy} + y'^2\phi_{yy}}. \tag{14}$$

A complete geometric characterization of any sectional family has been given by Annette Vassel.[5]

7. *Curvature Trajectories.*—To define *curvature trajectories*, we start with an arbitrary doubly infinite family of curves, that is, a general differential equation of second order $y'' = F(x, y, y')$. A curvature trajectory of this family is a curve which is drawn so as to have at each point c times the curvature of the member of the family to which it is tangent at that point, c remaining constant along the trajectory. For a given value of c there will be a set of ∞^2 trajectories, one in each direction through each point. By varying c, we obtain ∞^1 such sets. Hence a given doubly infinite family generates a triply infinite system of curvature trajectories.

The ∞^2 trajectories that can be drawn for a fixed value of the curvature ratio c satisfy the equation $y'' = cF(x, y, y')$ (since the curvature at a given lineal element is proportional to y''). Eliminating the parameter c by differentiation, we find that the complete system of ∞^3 trajectories is of the type G where

$$G = \frac{1}{F}(F_x + y'F_y), H = \frac{F_{y'}}{F}. \tag{15}$$

Such systems have been discussed in relationship to dynamical trajectories and sectional families.[6] We note that *every complete velocity system is a special case of curvature family.*

8. *The Additive-Multiplicative Trajectories.*—We shall first of all consider some elementary lineal element transformations of the plane. These are (1) the *turn* which has been considerably studied in our preceding work,

and (2) the *magnicline*, which has been recently introduced. A turn T_α is the result of rotating each lineal element about its point through a constant angle α, whereas a magnicline M_m is the effect produced by multiplying the inclination θ of each lineal element by the same constant number $m \neq 0$ while leaving its point fixed.

A turn may be considered to be an additive correspondence, while a magnicline is a multiplicate correspondence. The group generated by turns and magniclines is

$$X = x, \; Y = y, \; \Theta = a\theta + b, \tag{16}$$

where $a \neq 0$ and b are constants. This may be called the additive-multiplicative group. This is intrinsic, independent of axes.

By applying a single transformation of (16) to the lineal elements of a simple family of curves: $dy/dx = \tan f(x, y)$, we obtain the ∞^1 additive-multiplicative trajectories of the given family. By varying a and b, we obtain *the complete system of* ∞^3 *additive-multiplicative trajectories*. Any such system is given by a differential equation of the type G where

$$G = \frac{f_{xx} + 2y'f_{xy} + y'^2 f_{yy}}{f_x + y'f_y}, \; H = \frac{f_y}{f_x + y'f_y} + \frac{2y'}{1 + y'^2}. \tag{17}$$

Certain generalizations of these trajectories are being investigated by F. McMahon in my seminar.

In conclusion, we may note that all these problems with one single exception belong to the field of projective geometry. The single exception is the additive-multiplicative trajectories, obviously of metric character.

* Presented to the American Mathematical Society.

[1] Kasner, "Differential Geometric Aspects of Dynamics," *Princeton Colloquium Lectures*, 1912, 1934. Also *Trans. Amer. Math. Soc.*, 1906–1910.

[2] Terracini, "Differential Equations of the Type $y''' = Gy'' + Hy''^2$," *Revista di Matematica*, **2** (1941).

[3] Kasner and De Cicco, "Geometry of Velocity Systems," *Bull. Amer. Math. Soc.*

[4] Kasner, "Dynamical Trajectories and the ∞^3 Plane Sections of a Surface," *Proc. Nat. Acad. Sci.*, **17**, 370–376 (1931).

[5] Vassel, "Characterization of Sectional Families," *Am. Jour. Math.* (1939).

[6] Kasner, "Dynamical Trajectories and Curvature Trajectories," *Bull. Am. Math. Soc.*, 449–455 (1934); Comenetz, Curvature Trajectories, *Amer. Jour. Math.*, **58** (1936).

[7] Kasner, "Lineal Element Transformations Which Preserve the Isothermal Character," *Proc. Nat. Acad. Sci.*, **27**, 406–412 (1941); also *Revista de Matematicas y Fisica teórica*, **II** (1941) (Tucumán).

[8] Another important type of differential equation with many applications in calculus of variations and physics is $y = Ay'''^2 + By'' + C$. See Princeton Colloquium and a forthcoming paper by the author in *Revista di Matematica*.